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THE EFFECTS OF STARVATION ON PHOTOTAXIS AND SWIMMING OF LARVAE OF THE CRAB *RHITHROPANOPEUS HARRISII*

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The phototactic response pattern of the zoeal larval stages of crabs, which was described for *Rhithropanopeus harrisii* by Forward and Costlow (1974) and for various other light-adapted crabs by Forward (1977), is known to be altered by changes in environmental factors. Shifts in phototactic response have been described for *R. harrisii* larvae under conditions of altered salinity (Latz and Forward, 1977) and temperature (Ott and Forward, 1976), and for other species of crab larvae in altered pressure (Rice, 1964). It is likely that conditions in the internal environment also can influence phototactic behavior. Among these internal modifiers could be the nutritional condition of the larvae.

In other crustacean zooplankton, including larval forms, feeding or the presence of food has been reported to affect photobehavior. In *Daphnia magna*, Clarke (1932) found that positive phototaxis was minimal in media containing an abundance of food, but this effect could have been produced by the external medium. Lucas (1936) showed that the copepod *Eurytemora hirundoides* and the mysid *Neomysis* swam down, away from an overhead light, when in concentrated phytoplankton suspensions. On the other hand, Bainbridge (1953) reported that *Calanus finmarchicus* swam upward in overhead illumination when in the presence of phytoplankton. In the work of both Lucas (1936) and Bainbridge (1953), dark controls were not performed, so it is possible that the observed changes in vertical movement were not caused by a change in phototaxis. The most convincing work has been done with crustacean larvae. Singarajah *et al.* (1967) showed that starved stage-II nauplii of the barnacles *Eliminus modestus* and *Balanus balanoides* have enhanced positive phototaxis and reduced negative phototaxis when compared to fed nauplii. The differences were most pronounced when the experiments were done in the filtered media of algal cultures. Zoea larvae of the anomuran crab *Emerita analoga* also are more positively phototactic and less negatively phototactic when starved (Burton, 1979).

This paper describes experiments to determine the effects of feeding on phototaxis and swimming of zoea larvae of the crab *Rhithropanopeus harrisii* (Gould). Starved early-stage larvae showed increased positive phototaxis and in some cases reduced negative phototaxis. The swimming speeds in all stages were generally lower in starved larvae.

Materials and Methods

Larvae for all experiments were obtained from ovigerous specimens of *Rhithropanopeus harrisii* (Gould) collected from the Neuse River in eastern North Carolina. Crabs were maintained in filtered sea water at 25° C and 20‰ salinity

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and in a 12:12 light:dark cycle. Upon hatching, larvae were maintained in the same conditions as the female crabs in large finger bowls, and were transferred daily to clean sea water and fed newly hatched *Artemia salina* nauplii until used in experiments.

Phototactic behavior was monitored by placing larvae in a quartz cuvette and viewing them through a stereomicroscope coupled to a closed-circuit television system (described in detail by Forward, 1974). All experiments were begun 5 to 7 hr after the onset of illumination of the light:dark culture cycle. Viewing illumination was filtered to 802 nm with an interference filter (Optics Technology, Inc.; half band pass, 39 nm). This wavelength does not affect phototactic behavior (Forward and Costlow, 1974). Stimulus illumination was provided in the horizontal plane by a LeBelle slide projector with a 300 W tungsten bulb. Horizontal stimulation permits separation of phototactic responses from geotactic responses. Light was filtered by two hot mirrors (Baird Atomic) and a Corning #1–75 filter to reduce heat, and filtered to 500 nm by an interference filter (Ditric Optics, half band pass 7.4 nm). This wavelength was selected because it corresponds to the sensitivity maximum of the larvae (Forward and Costlow, 1974). Intensity of the stimulus was regulated by neutral density filters and was measured with a YSI model 65 radiometer. The duration of the stimulus was set at 2 sec and was controlled by an electromagnetic shutter (Uniblitz model 225XOROX5, with a model 310 drive unit).

Responses were recorded on video tape and analyzed as reported previously (Forward and Costlow, 1974). Positive phototaxis was defined as movement toward the stimulus source (± 15°), while negative phototaxis was movement 180° to the stimulus source (± 15°). Swimming direction and speeds for the dark control were determined immediately before the onset of a light stimulus. Swimming speeds were determined by measuring the curvilinear distance traveled in 0.5 sec. Results of these analyses were compared using standard analysis of variance techniques (Sokal and Rohlf, 1969).

In studies of phototaxis, all larvae were light-adapted under room lights plus a 60 W incandescent light for at least 1 hr prior to experimentation. Larvae were pipetted into the experimental cuvette and were used only once on any day. One min was allowed in total darkness on the microscope stage before the first stimulation; stimuli were then spaced at 15-sec intervals. The procedure used varied with each experiment and is described below.

Experiment 1—Effects of feeding and prey medium upon phototaxis

Larvae of stages I (4 broods) and III (3 broods) were used. Experimental stage-I larvae from each brood were fed for 1 day after hatching and then divided into two equal portions: the first was fed for a second day (fed group) while the second received no food (starved group). At the end of this second day, larvae were again changed to fresh 20‰ sea water and then each group was further subdivided into 2 groups; one placed in fresh filtered sea water of 20‰ and the other in a mixture of 20‰ filtered sea water mixed in equal parts with water in which *Artemia salina* nauplii had been hatched and reared for 24 hr, filtered and adjusted to 20‰ with distilled water. Thus there were 4 subgroups to be tested: fed—sea water; fed—"*Artemia* medium"; starved—sea water; and starved—"*Artemia* medium."

After 1 hr in the new medium, larvae in each subgroup were tested for phototaxis over the intensity range of 2.3×10^{-5} W/m^2 to 2.3 W/m^2 in 0.5 log unit steps. Each sample of larvae was stimulated at 4 intensities, either in ascending or descending order of intensity, and then discarded. Two larval samples from each brood were tested at each intensity. In order to study the effect of stage on the relationship between nutritional state and phototaxis, stage-III larvae were treated similarly to stage I, except that they were reared normally until the first day after the molt to the third zoeal stage. They were then divided into fed and starved groups and treated identically to the stage-I larvae.

Experiment 2—Ontogeny of effect of feeding upon phototaxis and swimming

The results of experiment 1 indicated different responses of stage-I and stage-III larvae to lack of feeding. In order to investigate whether this was due to an ontogenetic effect or to a difference in amount of food reserves in various stages, all four zoeal stages were tested for their phototactic response under fed and starved conditions. Originally, it was planned that each successive stage would be starved for a greater amount of time. However, it was found that after 3 days of starvation, the later-stage larvae were not suitable for testing due to high mortality and inability to swim well. Thus the starvation times for each stage were as follows: stage I, 1 day; stage II, 2 days; stage III, 3 days; stage IV, 3 days. If larvae of each stage are fed after these starvation times, they will generally show good recovery and low subsequent mortality. The rearing regime for stage I was identical to that used in experiment 1. For the later stages, on the morning following the molt to the desired stage the larvae were subdivided into fed and starved groups. Thereafter, each group was changed daily into clean water, tested, and the fed group given fresh *Artemia salina* nauplii. On the final day of testing, each group was further subdivided into sea water and "*Artemia* medium" subgroups, as in experiment 1, before testing. Because fed larvae typically molted to the next stage after 2 days, it was not always possible to test fed larvae on the second and later days in each stage.

Usually, larvae from three broods were tested at each stage, but four broods were used for stage II, day 1; and two broods used for stage III, day 3. Larvae were tested for positive phototaxis at an intensity of 6.0×10^{-2} W/m^2 and for negative phototaxis at an intensity of 6.0×10^{-4} W/m^2. These intensities were selected for evoking the desired response by reference to the results of experiment 1 and to the work of Forward and Costlow (1974). Each sample was tested only once at each intensity and then returned to clean sea water or discarded. Three samples were tested at each intensity for each brood. Swimming speeds were measured during random swimming, positive phototaxis and negative phototaxis.

Experiment 3—Ontogeny of feeding rate

In order to investigate the effect of time of day and of stage on larval feeding, 18 larvae from each of two broods were isolated within 2 hr of hatching into wells of glass spotting plates (average volume, 1.4 ml), and maintained until the molt to the first crab stage. Conditions were as for other experiments; that is, 25° C, 20‰ salinity, and a 12:12 L:D cycle. At the end of the light period and the end of the dark period they were observed under a dissecting microscope and the number of individual *Artemia salina* nauplii consumed in the preceding

TABLE I

Results of an analysis of variance on the effects of light intensity at 500 nm, nutritional state (fed vs. starved), and medium (20‰ sea water vs. "Artemia medium") on positive and negative phototaxis by first and third stage larvae. d.f. = degrees of freedom.

Source of variation	Zoea I			Zoea III		
	d.f.	Positive phototaxis (F value)	Negative phototaxis (F value)	d.f.	Positive phototaxis (F value)	Negative phototaxis (F value)
Light intensity	10, 132	56.05***	4.57***	10, 88	10.58***	2.71**
Nutritional state	1, 132	39.43***	4.22*	1, 88	0.70	0.02
Medium	1, 132	2.01	0.05	1, 88	0.26	0.65
Intensity × nutritional state	10, 132	0.79	1.44	10, 88	0.50	1.25
Medium × nutritional state	1, 132	0.48	0.21	1, 88	0.03	0.77
Intensity × medium	10, 132	0.51	0.56	10, 88	0.37	0.72
Intensity × nutritional state × medium	10, 132	0.33	0.71	10, 88	0.68	1.03
Error	132			88		
Total	175			131		

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

3- or 12-hr interval was noted. Observations during the dark period were made using a microscope lamp interference filtered to 700 nm, a wavelength to which the larvae are very insensitive, to provide as little visible light to the larvae as possible.

During the first 2½ days, the number of newly hatched brine shrimp nauplii was restored at the end of each 3-hr period to the number appropriate for the stage of that individual larva (see below). After each 12 hr throughout the experiment, the larvae were changed to fresh 20‰ sea water containing a number of newly hatched nauplii which was greater than the number of nauplii which could be consumed in 12 hr. Ten nauplii were supplied to each stage-I larva, 25 to stages II through IV, and 30 to each megalopa. The total number of nauplii consumed by each larva, the number consumed in each larval stage, and the difference between the number eaten at night and during the day were thus determined.

RESULTS

Effect of starvation on responses to a range of light intensities

In experiment 1, stage-I and stage-III larvae were tested for positive and negative phototaxis over a range of light intensities. Tests were performed in both filtered sea water and in "*Artemia* medium." The results of the experiments for each stage were analyzed by a 3-way ANOVA, with the main effects being light intensity, nutritional state, and medium (Table I). Both light intensity and nutritional state had significant effects on phototaxis in stage I, while in stage III only light intensity was significant. In each stage, the same main effects had statistically significant influences on both positive and negative phototaxis.

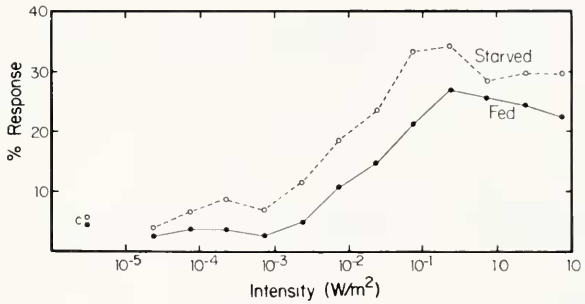

FIGURE 1. Per cent response (ordinate) of positively phototactic fed (closed circles, solid line) and starved (open circles, dashed line) stage-I zoea larvae to various intensities of 500 nm light (abscissa). The average sample size for each point is 366 larvae (fed) or 340 larvae (starved). C indicates the control level of response.

Since there was no significant effect of medium, data for all stage-I larvae were combined for each feeding condition and light intensity. The combined data show that in stage I, starved larvae were consistently more positively phototactic than fed larvae at all intensities tested (Fig. 1). The effect of light intensity was the usual one, leading to increased response at higher light intensities (Forward and Costlow, 1974). For negative phototaxis, starved stage-I larvae generally had a slightly reduced response compared to fed larvae (Fig. 2), particularly at the high intensities. Again, the pattern with respect to intensity for both starved and fed larvae was similar to that found by Forward and Costlow (1974) for negative phototaxis; *i.e.*, highest response to relatively low intensities (10^{-3}–10^{-4} W/m^2) for light-adapted larvae.

For stage-III larvae, both positive and negative phototaxis were affected significantly only by light intensity level, so the data for both nutritional states and both media were combined at each intensity. The overall pattern for both positive and negative phototaxis was the typical one described by Forward and Costlow (1974).

Effects of increasing length of starvation on phototactic response

Although stage-III larvae did not show altered phototaxis after 1 day of starvation, this could be because they have food reserves adequate to maintain

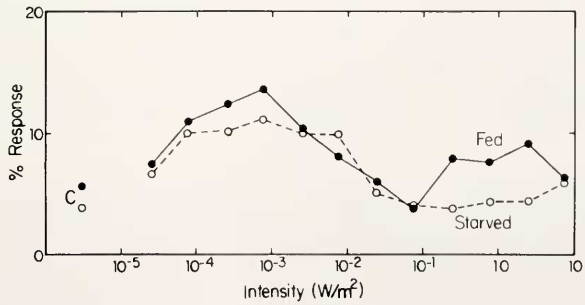

FIGURE 2. Per cent response (ordinate) of negatively phototactic fed (closed circles, solid line) and starved (open circles, dashed line) stage-I zoea larvae to various intensities of 500 nm light (abscissa). The average sample size for each point is 366 larvae (fed) or 340 larvae (starved). C indicates the control level of response.

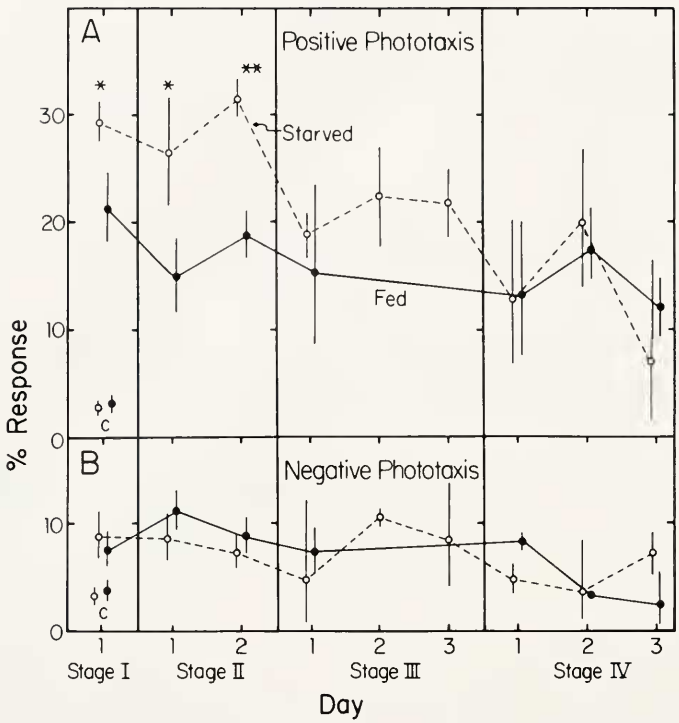

FIGURE 3. Per cent phototaxis (ordinate) vs. stage and day (abscissa) for the zoeal stages of crab larvae fed (closed circles, solid lines) or starved (open circles, dashed lines) for various amounts of time. Each point shows the standard error for, usually, 3 broods of larvae (see text). Positive phototaxis is shown in A, negative phototaxis in B. Significantly different responses between fed and starved larvae (one-tailed t-test) are indicated by asterisks above the significantly different pair ($* P < 0.5$; $** P < 0.01$). C indicates the control level of response. The sample size for each point ranged from 46 (positive phototaxis, starved, stage III, day 3) to 357 (positive phototaxis, fed, stage I, day 1).

them in good nutritional condition for longer than 1 day. According to this view, the behavior of the larger late-stage larvae would change at a slower rate with starvation time than that of earlier stages. To test this hypothesis, fed and starved larvae of each successive stage were tested for increasing numbers of days. On the final day of testing for each stage, the effect of medium on positive and negative phototaxis of fed and starved larvae was also tested. In no case was the effect of medium found to be significant ($P > 0.05$), so all data for larvae in sea water and "*Artemia* medium" were combined for portrayal and further analysis.

In stages I and II, positive phototaxis of starved larvae significantly exceeded that of fed larvae (Fig. 3). Although in stage III the mean level of positive phototaxis of starved larvae was always higher than that of fed larvae, there were no statistically significant differences between positively phototactic responses of starved and fed larvae in stages III and IV. Similarly, although positive phototaxis on the second day of starvation always exceeded that on the first day, no statistically significant trends were found in change of level of positive phototaxis with increasing starvation time.

With regard to negative phototaxis, there was no indication of a starvation effect at any time, not even in stage I. The results thus differ from those of

experiment 1; this was probably because negative phototaxis was measured at only one intensity; note in Figure 1 that negative phototaxis was reduced the most at high light intensities.

Starvation and swimming speeds

The results of experiment 2 were analyzed for swimming speeds as well as phototaxis (Fig. 4). When swimming in the dark was being measured, starved

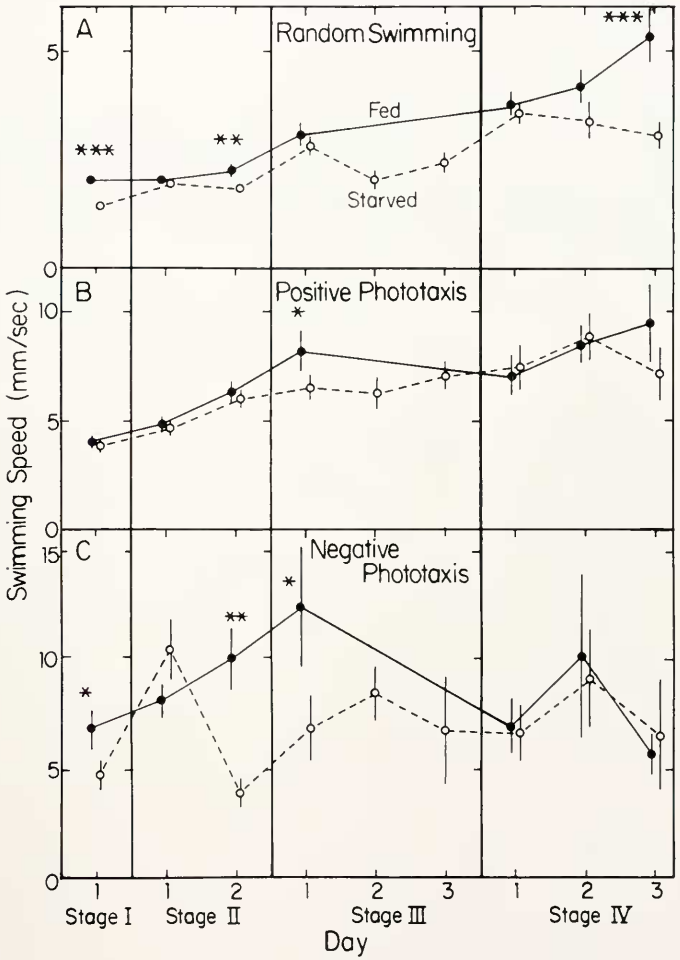

FIGURE 4. Swimming speeds in mm/sec (ordinate) of zoeal stages of crab larvae fed (closed circles, solid lines) or starved (open circles, dashed lines) for various amounts of time (abscissa). Each point shows the mean ± standard error for larvae in each condition. Random swimming (no stimulus) is shown in A, swimming in positive phototaxis in B, and swimming in negative phototaxis in C. Significant differences between fed and starved larvae (one-tailed t-test) are indicated by asterisks above the significantly different pair (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). The sample size for each point depended upon the number of larvae responding in positive and negative phototaxis; it ranged from 43 (starved, stage IV, day 2) to 141 (starved, stage I, day 1) for random swimming; from 9 (starved, stage IV, day 3) to 78 (fed, stage I, day 1) for positive phototaxis; and from 3 (fed, stage IV, days 2 and 3) to 30 (fed, stage I, day 1) for negative phototaxis.

larvae always swam more slowly than fed larvae; the difference, as tested by a t-test (one-tailed) for each day, was significant for stage I, day 1; stage II, day 2; and stage IV, day 3. During positive phototaxis, swimming speeds of fed larvae again usually exceeded those of starved larvae, but the effect was only significant for larvae in stage III, day 1. Swimming speeds of fed larvae during negative phototaxis were also usually higher than those of starved larvae; the difference was significant for stage I, day 1; stage II, day 2; and stage III, day 1. There was little evidence in any of the conditions measured that speed of swimming in larvae decreased further as they were starved for longer periods; only once (stage II, negative phototaxis, $P < 0.001$) did swimming speed significantly decline as starvation progressed.

Time of day and larval feeding

The average number of individual *Artemia salina* nauplii consumed per 12-hr period (night or day) is shown in Figure 5. Only time periods which did not include a molt and only larvae which completed metamorphosis to the first crab stage (n = 32) were used in the analysis. The results of a 2-way ANOVA on

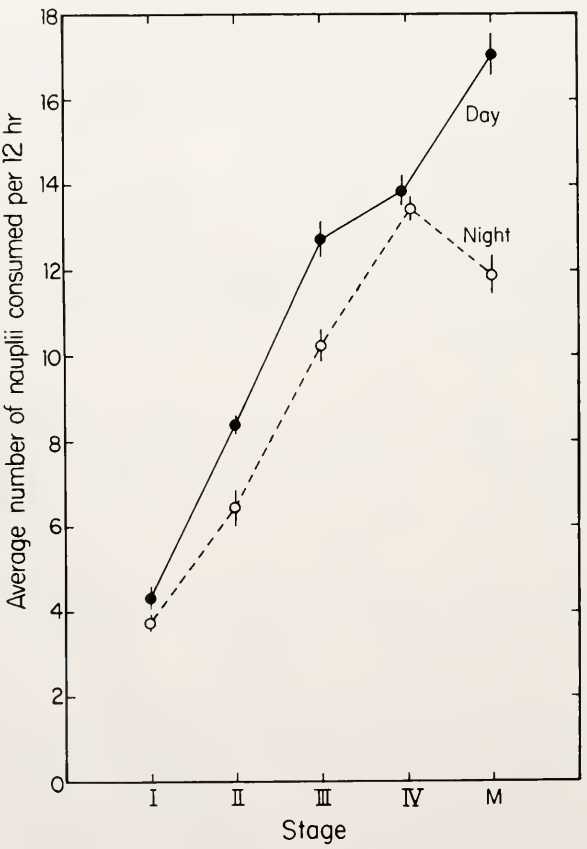

FIGURE 5. Average number of newly-hatched *Artemia salina* nauplii (ordinate) consumed by crab larvae at various stages (abscissa) during the day (closed circles, solid line) or night (open circles, dashed line). Each point shows the mean and standard error for 32 larvae.

TABLE II

Results of an analysis of variance on the effects of larval stage (zoea 1 through megalopa) and time of day (day vs. night) on the number of brine shrimp nauplii consumed in a 12-hr period. d.f = degrees of freedom.

Source of variation	d.f.	F Values F
State	4, 310	397.346***
Time of day	1, 310	86.8825***
Interaction	4, 310	13.9951***

*** $P < 0.001$.

this data are included in Table II; both of the main effects of stage and time of day were highly significant. The effect of stage was seen as a rapid increase in consumption of nauplii with each molt, while the time effect was a greater feeding rate during the day as compared to night.

The differences in consumption with time of day were somewhat different in the three earliest stages, with more nauplii eaten during the day, from stage IV, in which daytime and nighttime rates were very similar. The megalopa showed the greatest difference between daytime and nighttime rates, consuming 143% as many napulii during the day as during the night.

DISCUSSION

Early-stage (first and second zoea) *Rhithropanopeus harrisii* larvae showed enhanced positive phototaxis when they were starved for a day or more. This change in phototaxis was not seen in the later, third- and fourth-stage zoea larvae. Also, upon stimulation with high light intensities, stage-I larvae had a reduced level of negative phototaxis after starvation.

In contrast to some earlier studies of planktonic crustaceans and crustacean larvae (Bainbridge, 1953; Clark, 1932; Singarajah *et al.*, 1967), the nature of the test medium did not affect either phototaxis or swimming speeds. Larvae of *R. harrisii* are sensitive to the medium in which they are living, as they are very responsive to changes in salinity (Latz and Forward, 1977); and we have often noted that day-old larval cultures become more responsive to an incandescent light source following tranfer to clean 20‰ sea water. It is possible that they are also sensitive to exudates of some prey forms but not to those of *Artemia salina* nauplii, admittedly not a normal food item.

The general pattern of an increased level of positive phototaxis and/or a reduction in negative phototaxis in starved animals has now been demonstrated for a variety of planktonic crustaceans, particularly larval forms. Clarke (1932) noted that *Daphnia magna* was most photonegative when living in fresh cultures containing plenty of food; however, this could have been an effect of the medium. Singarajah *et al.* (1967) showed that nauplii of the barnacles *Eliminus modestus* and *Balanus balanoides* had both an increase in photopositive behavior and a decerase in photonegativity when they were starved, as compared to the fed controls. Unlike the situtation for *R. harrisii* larvae, these starved barnacle nauplii were even more photopositive when tested in media from the food cultures.

Among larvae of crabs, first-stage zoea larvae of the mole crab *Emerita analoga* became increasingly photopositive during starvation from 2 to 4 days; fed larvae,

on the other hand, became more negatively phototactic over this period (Burton, 1979). Although the level of positive phototaxis of *R. harrisii* larvae increased on the second day of starvation in stages II, III, and IV, this increase was not statistically significant and the pattern of change in negative phototaxis is irregular. Thus, there is little evidence that increasing the duration of starvation potentiates its effect on phototactic behavior in *R. harrisi* larvae.

In *R. harrisii* larvae, the starvation effect is mostly an enhancement of positive phototaxis; negative phototaxis is affected much less than positive in stage I (the effect being seen mostly at higher light intensities) and not at all in the later stages. The change could be because of greater energy stores in the later stages; in fact, some stage-IV larvae starved for longer than 3 days successfully molted to the megalopa. Alternatively, the phototactic pattern could be more conservative in later stages; Latz and Forward (1977) have found that the change in phototactic pattern with changing salinity is more extreme in stage-I *R. harrisii* larvae than in stage IV.

The swimming of starved larvae was generally slower than that of well-fed larvae from the same brood. The difference in speed was most evident during negative phototaxis, when fed larvae reach their maximum speeds (Forward and Costlow, 1974). The amount of reduction of swimming speeds in starved larvae is generally quite constant with increased time of starvation in a given stage; only in stage II is there a significant change in swimming speed after the first day of starvation. This generally decreased activity level during starvation is probably a result of energy conservative mechanisms, and not deteriorative effects, as late-stage larvae will survive up to 3 days of starvation with good recovery on subsequent feeding.

Feeding rates in *R. harrisii* larvae are known to decline at concentrations of *Artemia salina* nauplii lower than 2 to 5 nauplii per ml (Welch and Sulkin, 1974), but the concentrations used in this study exceeded this level (minimum initial concentration: 7.1 nauplii per ml). Therefore, the larvae were probably consuming prey at a maximum rate. This is also suggested because many of the nauplii taken as prey were only partly eaten. Often only the yolk-rich posterior portion was consumed and the anterior portion with its swimming appendages discarded. This was perhaps partly because crab larvae usually consume nauplii prey from the abdomen forward, and when the nauplius is held in this position, its swimming appendages are immoblized. Sulkin (1975) and Sulkin and Norman (1976) have suggested that the lipid yolk material stored in the abdomen region of *Artemia* nauplii is important for development in crab larvae.

When placed in a light : dark cycle, *R. harrisii* larvae consume more food during the 12-hr light phase than during the equal period of dark. However, zoea larvae continue to take in from 43 to 49% of their total daily food during the night, and the megalopa consumes 41% of its daily intake at night. The fact that feeding activity continues to occur at night suggests that visual orientation to prey is not essential for feeding and that the slightly depressed nighttime feeding levels probably reflect a generally lowered feeding activity. Although crab larvae have been reported to show a directed strike behavior (Knudsen, 1960), they are thought not to use sight to localize prey (Gonor and Gonor, 1973). For example, larvae of *Uca pugilator* apparently locate and trap prey by a mechanical tail-lashing technique (Herrnkind, 1968). Since *R. harrisii* larvae feed less at night, the possibility of their photobehavior being altered by feeding state is strongest in the

early part of the day, and at this time they could show the highest levels of positive phototaxis. This has not been tested, but any effect is probably very slight.

The overall effects of starvation on phototaxis of *R. harrisii* larvae will probably bring them nearer to the surface in a natural water column, where food is presumably more abundant. This would also tend to move them to other parts of the estuary, where more abundant food supplies might be encountered. But it would simultaneously increase the rate of their transport by currents toward the mouth of the estuary in which they are living. In addition, starved larvae will be much more vulnerable to visually oriented predation, and since their swimming speeds are reduced they will have less chance of escape. The reduction of negative phototaxis in stage I could also be important, since this would reduce the shadow response which is probably used to avoid drifting cnidarian and ctenophore predators (Forward, 1976, 1977). Because both the response level and the swimming speeds are reduced in stage-I larvae during negative phototaxis, they will be particularly susceptible to this type of predation. On the other hand, most of the reduction in negative phototaxis occurs at higher light intensities, but the shadow response is most active at quite low intensities (Forward, 1976), so this response will remain somewhat effective.

Once fed, the larvae of all stages will probably regain the response pattern typical of well-fed larvae and move down in the water column. This migration pattern would be very similar to that described for *Sagitta elegans* by Pearre (1973), in which the chaetognaths swam downward when satiated, but remained near the surface, particularly at night, when hungry. One important difference between *S. elegans* and *R. harrisii* larvae, however, is that in the chaeteognaths feeding occurs mainly at night, but the crab larvae consume most of their food during the day.

The phototactic response pattern of crab larvae is sensitively tuned to the environment. Changes in the external environment alter phototaxis, as shown for salinity (Latz and Forward, 1977) and for temperature (Ott and Forward, 1976). To these external influences can be added the internal modifier of nutritional state.

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Summary

1. Stage-I zoea larvae became more positively phototactic and less negatively phototactic after 1 day of starvation. Stage-II larvae also had an increased positive phototaxis after 1 or 2 days of starvation, but their negative phototaxis was not changed. Later stages did not have altered phototaxis during starvation.

2. The swimming speeds of starved larvae were generally lower than those of fed larvae, but there was no further reduction in the swimming speed after the first day of starvation.

3. When kept in a 12 : 12 light : dark cycle, larvae of all stages consumed more food during the day than at night, but feeding in the dark was still effective. Therefore, there probably is little effect of nutritional condition on phototaxis over the course of a day.

4. The altered phototaxis of starved larvae would move them higher in the water column, where food is presumably more abundant, and would also increase their opportunity to be carried into new regions of an estuary where they could encounter food. However, the reduced negative phototaxis and lowered swimming speeds of starved larvae probably would place them in increased risk of both predation and export from estuarine waters.

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